

Phylogeny of the Genera of Ticoplinae (Hymenoptera: Mutillidae)

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Abstract.—The subfamily Ticoplinae Nagy is one of the more basal taxa in Mutillidae. Cladistic analyses using 21 characters have demonstrated that recognition of two tribes is supported. Ticoplini Nagy includes *Nanomutilla* André (= *Ticopla* Nagy *syn. nov.*) and *Arcotilla* Bischoff; Smicromyrmillini Argaman includes *Smicromyrmilla* Suárez (and possibly *Camerouilla* Lelej and Krombein, *Eosmicromyrmilla* Lelej and Krombein, and *Hindustanilla* Lelej and Krombein, should these be considered valid). The subfamily and tribes are reviewed and characterized, a key to tribes and genera is provided, and both sexes of typical members of the three main genera are illustrated. *Nanomutilla nadae* Argaman 1988 is selected as the correct spelling for the species also spelled *N. nada* in its original description, and *Arcotilla ferruginca* Mitchell and Brothers 1998 for the species also spelled *Arcotilla ferruginata* in its original description.

Ticoplinae Nagy 1970 is one of the relatively basal subfamilies of Mutillidae, as shown by Brothers (1975, 1999) (Fig. 1) and by Lelej and Nemkov (1997) whose analyses differed from Brothers' in several respects. It was established as a subfamily of Nagy's Heterogynidae (properly Heterogynidae; International Commission on Zoological Nomenclature 1987), to accommodate the genus *Ticopla* Nagy 1970, known only from male specimens. Brothers (1975) transferred Ticoplinae to Mutillidae, and Day (1984) placed *Heterogyn* Nagy in Sphecidae s.l.; it is now considered to comprise a distinct family, Heterogynidae (Brothers 1999, Melo 1999). The genera placed in Ticoplinae by Brothers (1975) were *Arcotilla* Bischoff 1920, *Nanomutilla* André 1900, *Smicromyrmilla* Suárez 1965 and *Ticopla*. Independently, Suárez (1975) proposed a new subfamily, Nanomutillinae, to contain *Nanomutilla*, and placed *Smicromyrmilla* in Myrmillinae but he did not realise that *Ticopla* or *Arcotilla* were of relevance. Brothers' (1975) study settled much of the controversy over the classification of these genera by showing

that they belong in a single subfamily, the valid name of which is Ticoplinae (and would remain so even if *Ticopla* were considered a junior synonym of *Nanomutilla*; International Commission on Zoological Nomenclature 1999: Article 40.1). He also concluded that the relationships amongst the component genera were such as to preclude the recognition of tribal divisions. However, Argaman (1988) proposed such divisions: Ticoplini, including *Ticopla* and *Nanomutilla*, which he considered distinct, and Smicromyrmillini, including *Smicromyrmilla*. He did not examine *Arcotilla*.

The cladistic study presented here elucidates the phylogeny of the genera of Ticoplinae, enabling objective assessment of Argaman's tribal divisions. The morphological terms used are those of Gauld and Bolton (1988). Specimens examined are in the collection of one of the authors (DJB) or were borrowed from numerous institutions (particularly the Natural History Museum (London) and Muséum National d'Histoire Naturelle (Paris)) over many years.

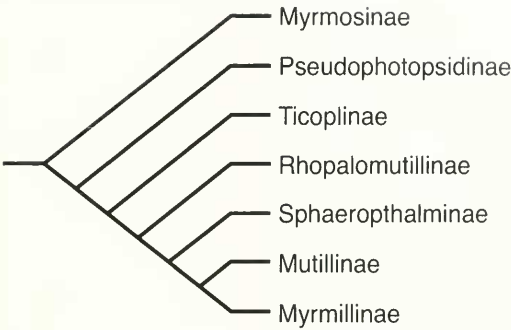


Fig. 1. Phylogeny of subfamilies of Mutillidae (simplified from Brothers 1975, 1999).

GENERA OF TICOPLINAE

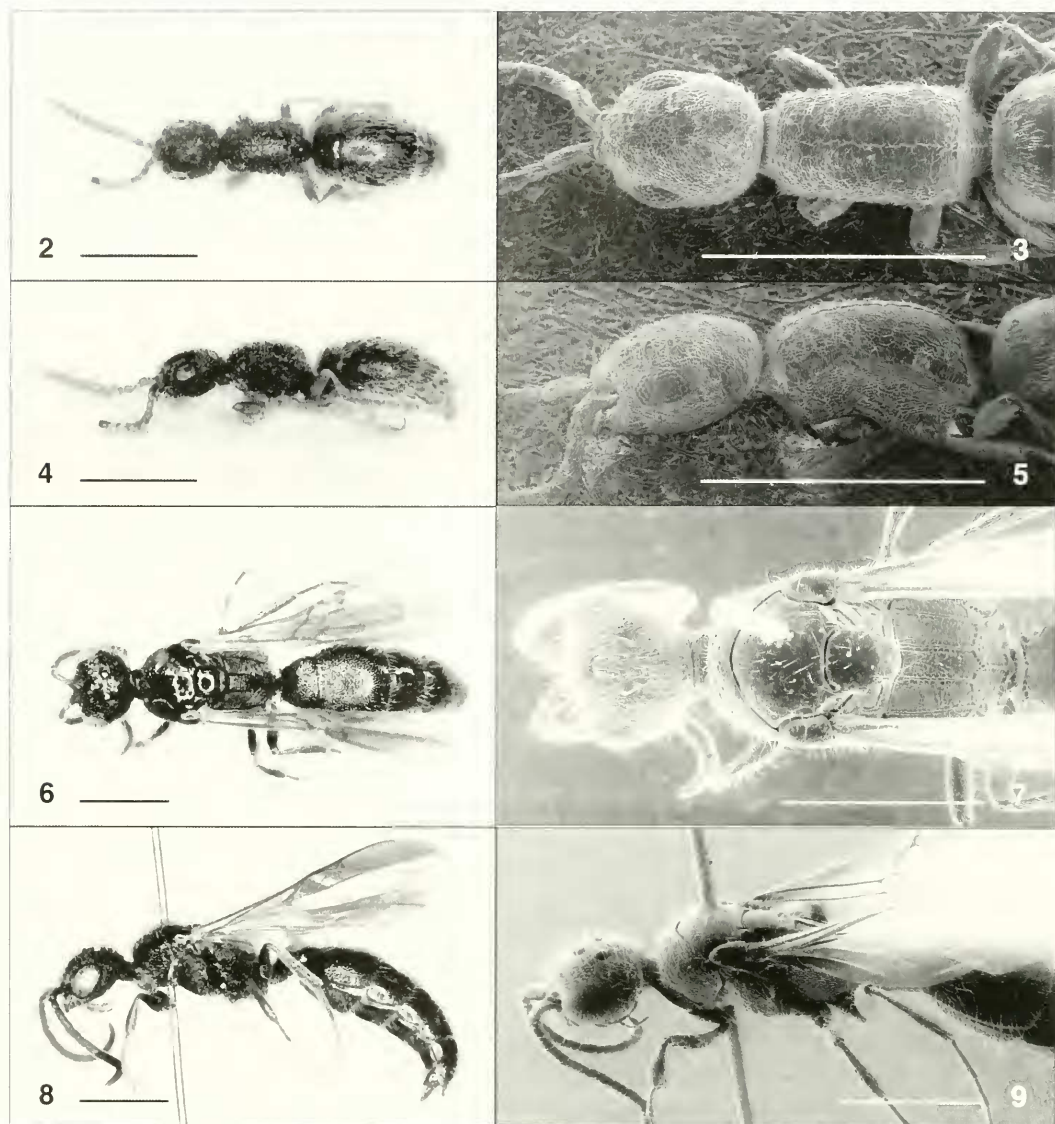
Nanomutilla André
(Figs. 2–9)

- Mutilla* (*Nanomutilla*) André 1900: 130.
Type species: *Mutilla vaucheri* Tournier 1895, Morocco, by subsequent designation of Ashmead (1903).
- Ticopla* Nagy 1970: 85.
Type species: *Ticopla yoca* Nagy 1970, Jordan, by original designation. **Syn. nov.**

The first description of *Nanomutilla* appeared in a key to subgenera of *Mutilla* published in April 1900, without any mention of included species. Later, in the same work, André (1901b: 223) presented a formal description based on a single species known from females only (*Mutilla vaucheri*) but also provided a description of the male in a footnote (p. 224), based on a second species supposedly known from both sexes (*Mutilla microsoma*) which he had recently described; it must thus be concluded that there were two originally-included species, although subsequent authors have considered *Nanomutilla* to have been a monotypic genus at establishment. André (1901a) described both sexes of *Mutilla* (*Nanomutilla*) *microsoma* from South Africa, being under the impression that the male and female specimens had been collected in the same area, Willowmore (“... j’ai trouvé une autre espèce du même sous-genre ... accompagnée d’un mâle rencontré dans les mêmes parages”). This, along

with their similarity in size, convinced him that the two specimens were conspecific, despite the fact that they were not captured *in copula*. We have examined the type series of *M. (N.) microsoma* in the Transvaal Museum and found that the female specimen was actually collected at Bothaville, in the Free State, while the male was collected near Willowmore, in the Eastern Cape, approximately 700 km away. They are not conspecific, nor even congeneric; Nonveiller (1973) concluded that the male really belongs in *Smicromyrmilla*. To add to the confusion, Bischoff (1921) described six new species of *Nanomutilla* without examining the type species; all of his new species would later be recognised as belonging in *Smicromyrmilla* (Nonveiller 1973). Not surprisingly, Arnold (1946, 1960) made the same error in describing another two species. Nonveiller (1973) transferred to *Smicromyrmilla* all species of *Nanomutilla*, except for *N. vaucheri* and the female of *N. microsoma*, and delimited both genera, although he had also not examined the type specimen(s) of *N. microsoma*. We confirm Nonveiller’s conclusions as correct. Argaman (1988) described a third species, *N. nadae* from Spain, again known only from female specimens. (Although the name is mostly spelled “*nada*” in that paper, it is “*nadae*” in the key; there is a statement that the species is named after Mrs Nonveiller, using her nickname [which is Nada, DJB pers. obs.], so the feminine genitive form is preferable, and the commoner spelling is probably an inadvertent error.)

Many statements by other authors referring to *Nanomutilla* have been based on a presumption that they apply to the type species, *N. vaucheri*. It is now clear to us, however, that the specimens identified and illustrated as *N. vaucheri* by Nonveiller (1973), Argaman (1988), and possibly Suárez (1975), were misidentified, although they were also collected in Morocco (the type locality of *N. vaucheri* being Tangier). When compared with the origi-



Figs. 2-9. *Nanomutilla* spp., dorsal and lateral views. 2-5, *N. vaucheri* (Tournier), ♀, length = 2.0 mm (Gibraltar, compared with holotype). 6-9, *N. sp.*, ♂, length = 4.4 mm (Zimbabwe). Scales = 1.0 mm.

nal description (Tournier 1895) and the fuller description and illustration by André (1901b), some discrepancies are obvious. Both Tournier and André referred to a median longitudinal carina on the mesosoma (this is shown in André's illustration as ending in a fine tooth posteriorly) and also stated (and illustrated) that the mesosoma was twice as long as wide. The illustrations given by Nonveiller (1973)

and Argaman (1988) show the mesosoma as much less slender, without a complete longitudinal carina and without a median posterior tooth; Suárez (1975) expressed puzzlement at the lack of such a carina in specimens he identified as *N. vaucheri* but provided no illustrations. One of us (DJB) has examined the holotype of *N. vaucheri* (collected at Tangier by Vaucher, with Tournier's determination label referring to

the publication of the name, labelled as from the Tournier Collection and housed in the Geneva Museum). Unfortunately, it has been glued dorsal-side down to a card so that the dorsal surface of the mesosoma is almost entirely obscured. There is, however, a clearly conspecific specimen in the same collection, also collected at Tangier (in 1896), which is essentially identical to the holotype (although with the tibiae very slightly paler); the mesosomal dorsal surface is clearly visible and shows an almost complete very fine median longitudinal carina ending in a very small posterior tubercle, and the mesosoma is relatively more elongate than in the specimens illustrated by Nonveiller (1973) and Argaman (1988). Another specimen, from Gibraltar and housed in the Natural History Museum, London (illustrated here, Figs. 2–5), is also clearly conspecific although the appendages are slightly paler than in the holotype; it has lost the scattered long erect setae on the mesosoma and most of the decumbent pubescence, but shows the carina and tubercle more clearly as a result. The carina is extremely fine and somewhat irregular, normally concealed under fairly dense diagonally oriented decumbent pubescence that gives the appearance of a mid-dorsal line in unworn specimens, and even when visible needs careful illumination; Suárez (1975) may thus have overlooked it, although he did comment on the pubescent line. Both species of *Nanomutilla* illustrated and discussed by Argaman (1988) are different from the true *N. vaucheri* in all of the features listed by him as important in species differentiation, and, since the specimen he considered to be *N. vaucheri* was obtained from Nonveiller, it is clear that Nonveiller (1973) also misidentified the species. (Of four specimens now in the Paris Museum identified as *N. vaucheri* by André, only one (from Gibraltar, obtained from Saunders and thus almost certainly collected at the same time as the specimen in the London Museum) is correctly identified; the

others, one from Algeria and two from Syria, represent two different species.)

Ticopla was described for two new species collected in the Jordan region and known only from males (Nagy 1970). Brothers (1975) suggested that one of these may be the male of *N. vaucheri*, supposedly known from the same area but only from females (based on specimens so identified by André, see above). Argaman (= Nagy) (1988) countered this by describing females of both species of *Ticopla*. Nonetheless, he stated that “the resemblance between *Nanomutilla* and *Ticopla* females is so remarkable, and the difference so delicate, [that it is] entirely understandable” that André had identified a specimen from Syria (that Argaman called a *Ticopla*) as *N. vaucheri*; i.e., Argaman (1988) stated that these genera are so similar as to be easily confused.

We have examined five specimens (three females from Syria and two males from Amman, Jordan) that are unquestionably *Ticopla* based on Argaman's (1988) criteria, and find no consistent differences between them and female specimens of 6 further species from Gibraltar and Morocco (*N. vaucheri*) and southern Africa (including *N. microsoma*), and males of 17 species from Kenya and Angola to southern Africa. The differences in the sculpturing of the mesosomal dorsum of both sexes, the main character used by Argaman in distinguishing these two genera, are by no means as distinct as he supposed, since intermediate forms occur. Other differences given by Argaman, such as the shape of the flagellomeres, depend on the angle at which the specimen is viewed. Loss of the second submarginal cell (1S), thought characteristic of *Ticopla* by Brothers (1975), is also not significant since different degrees of reduction in wing venation are evident. We thus have no hesitation in regarding *Nanomutilla* and *Ticopla* as synonymous. Lelej and Krombein (2001) also regarded *Ticopla* as a synonym of *Nanomutilla*, implying that they

were following Argaman (1988) in this (which was incorrect since Argaman clearly stated that he considered them distinct, see above); it is probable that they were really following the suggestion made by Mitchell and Brothers (1998). The genus has an extensive distribution in the Afrotropical and southern Palaearctic (Iberian peninsula, Morocco, Algeria, Levant) Regions, most species being as yet undescribed.

***Arcotilla* Bischoff**
(Figs. 10–17)

Arcotilla Bischoff 1920: 25, 174.

Type species: *Arcotilla arcolata* Bischoff 1920, Transvaal, by original designation.

This genus was based on the type species and *A. marshalli* (André 1903). It is the smallest genus in the subfamily in terms of species numbers, and has been revised by Mitchell and Brothers (1998). It comprises eight species known from males and two known from females, all from southern Africa. (It should be noted that the correct spelling of the name for the new species referred to as *A. ferruginea* (in the text) and *A. ferruginata* (in a figure caption) by Mitchell and Brothers (1998) should be *A. ferruginea*; the *lapsus* is regretted.)

***Smicromyrmilla* Suárez**
(Figs. 18–25)

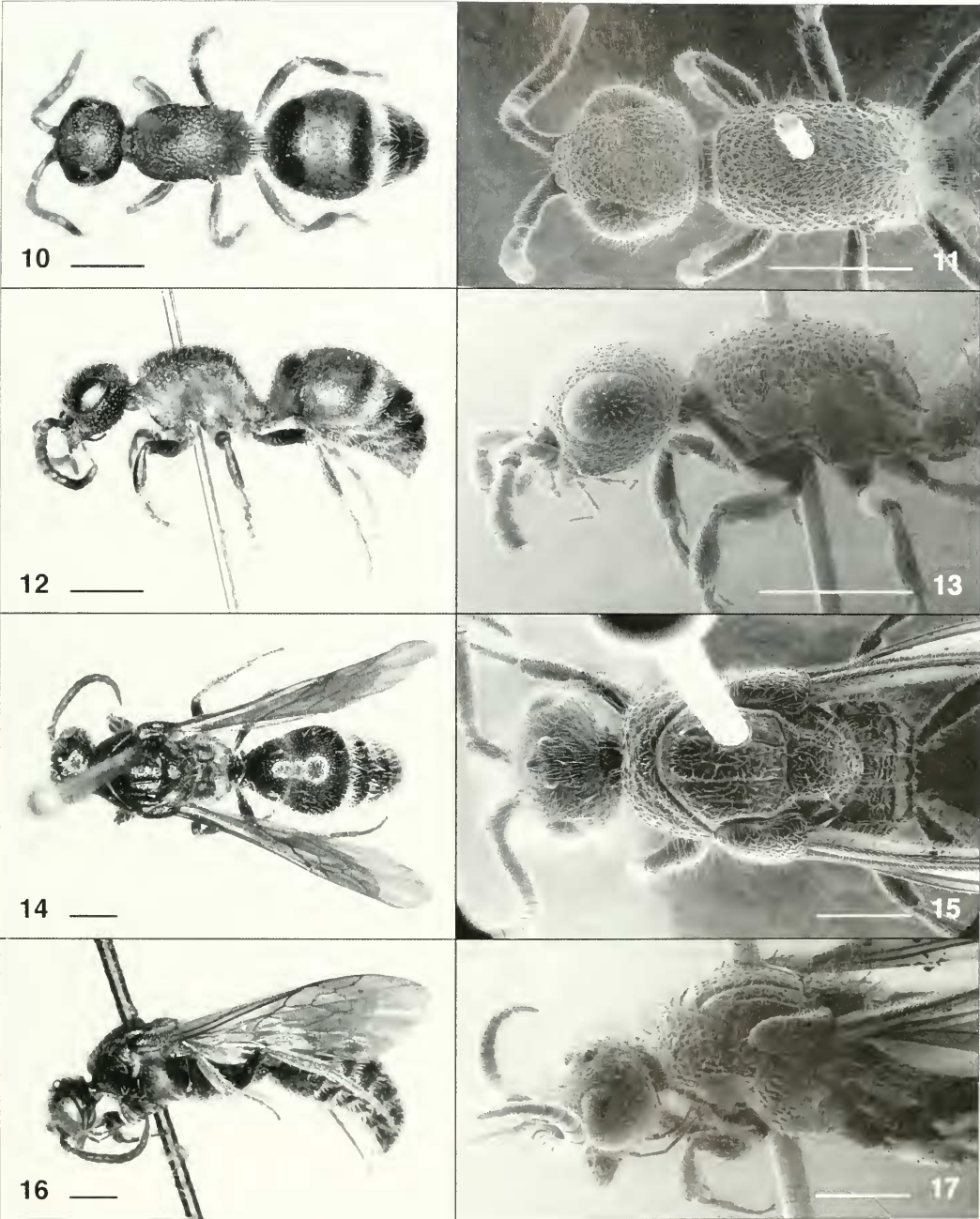
Smicromyrmilla Suárez 1965: 570.

Type species: *Mutilla ariasi* André 1896, Spain, by original designation.

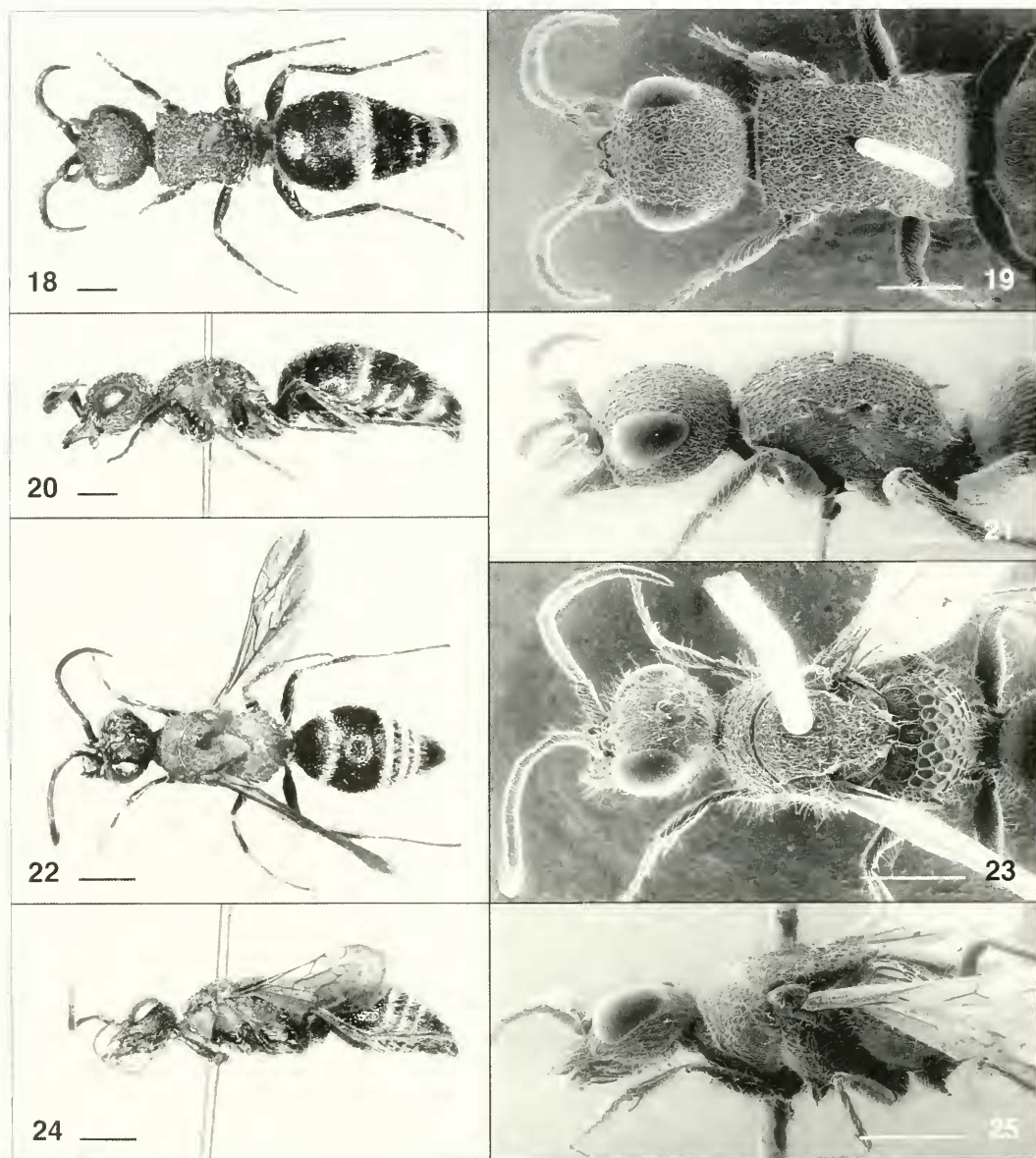
This genus was described for a single species (and single female specimen), although a second species from Spain, *Smicromyrmilla miranda* Nonveiller and Gros 1996, based on a single male specimen, has since been described; these are the only specimens recorded from that country, and may thus be conspecific. Nevertheless, many other species of *Smicromyrmilla* have been described and even more await description; they were being revised

by Nonveiller (pers. comm.) before his recent death. The genus exhibits considerable morphological variation (it is the only ticopline genus in which brachypterous and apterous males are known) and is widely distributed throughout the Afrotropical, southern Palaearctic (Spain, North Africa) and Oriental Regions.

After this paper had been accepted for publication, Lelej and Krombein (2001) described three new genera of *Smicromyrmillini* (*Cameronilla*, *Eosmicromyrmilla* and *Hindustanilla*) from the Oriental Region and provided a key for their recognition. For our study we had examined an apterous male of one of these genera (*Hindustanilla*) and considered it to be a *Smicromyrmilla*, although a somewhat anomalous one. We had also examined several Afrotropical species with characteristics different from those Lelej and Krombein considered limited to *Smicromyrmilla*, but again did not consider them as generically distinct. We recognised that *Smicromyrmilla*, as we conceived it, was quite variable, but saw independent variation in several of the characters used by Lelej and Krombein (2001) to distinguish their new genera, with many intermediates making recognition of new putative genera questionable. For this reason, we do not distinguish between *Smicromyrmilla* and the new genera proposed by Lelej and Krombein (2001), but do not wish to synonymise them formally. As far as we can ascertain, those genera agree with *Smicromyrmilla* in all of the characters we have used in this analysis. (We also suspect, however, that *Cameronilla* may not actually be a ticopline. Lelej and Krombein based their conclusions entirely on the rather inadequate original description and figure of the female of *Mutilla oedipus* Cameron 1897 in placing it in this subfamily, citing the presence of a median and lateral spines on the propodeum. Those characteristics would not preclude its placement in Myrmillinae, however,



Figs. 10–17. *Arcotilla* spp. 10–13, *A. ferruginea* Mitchell and Brothers, ♀, length = 4.9 mm (paratype, South Africa, KwaZulu-Natal). 14, 16, *A. marshalli* (André), ♂, length = 7.7 mm (holotype, South Africa, Northern Province). 15, 17, *A. vulgaris* Mitchell and Brothers, ♂, length = 8.9 mm (paratype, South Africa, Eastern Cape). Scales = 1.0 mm.



Figs. 18–25. *Smicromyrmylla* spp. 18–21, *S.* sp., ♀, length = 8.4 mm (South Africa, Mpumalanga). 22–25, *S.* sp., ♂, length = 6.5 mm (South Africa, Gauteng). Scales = 1.0 mm.

which placement is also suggested by its enlarged quadrate head.)

MATERIALS AND METHODS

Specimens of all available species of Ticoptinae (*Arcotilla*: 8 species based on males, 2 on females; *Nanomutilla*: 18 on males, 8 on females; *Smicromyrmylla*: 21 on

males, 8 on females) were surveyed. Of the more than 40 morphological characters examined, 21 (Appendix 1) had appropriate levels of variation (i.e. they were found to be variable among but not within genera) and were used in cladistic analyses. Character polarity was established by out-group comparison. When there was vari-

Table 1. Data matrix for analysis of genera of Ticoplinae using 21 characters of Appendix 1.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
Ancestor	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Areotilla</i>	0	0	0	1	0	1	1	1	0	1	1	0	1	0	1	1	0	1	1	0	0
<i>Nanomutilla</i>	0	0	0	1	0	0	0	0	0	0	2	1	1	0	1	0	1	1	1	0	0
<i>Smicromyrmilla</i>	1	1	1	0	1	0	1	0	1	1	0	0	0	1	0	1	0	2	0	1	1

ation among out-group taxa, *ad hoc* parsimony analysis was used to determine the plesiomorphic state; this is discussed, where applicable, below. Maximum-parsimony analysis was carried out using the software package Hennig86 version 1.5 (Farris 1988) (command ie*), and analysis using implied weights (Goloboff 1993) was done using Pee-Wee version 2.1 (Goloboff 1994) (commands hold* search=hold/20 mult*15). A hypothetical ancestral taxon was included, with all character states coded "0", to root the tree. Trees were analysed using Clados version 1.6.1 (Nixon 1994).

Out-group selection presented some difficulties, as the sister group of the Ticoplinae consists of the Rhopalomutillinae, Sphaerophthalminae, Mutillinae and Myrmillinae (see Fig. 1), i.e., most of the diversity of the family. In addition, these subfamilies all tend to show a greater proportion of apomorphic characteristics than does the Ticoplinae, and their usefulness is therefore lessened, particularly in the case of the Rhopalomutillinae, which has a comparatively large proportion of derived characteristics. We expected that

more accurate determination of character polarity would be obtained by including more relatively basal groups in the out group; thus the out group comprised four genera: *Myrmosa* Latreille (about 5 species examined) and *Myrmosula* Bradley (about 2 species) (both Myrmosinae), *Pseudophotopsis* André (about 10 species) (Pseudophotopsidinae) and *Dasylabris* Radoszkowski (about 15 species) (Sphaerophthalminae). The plesiomorphic state is that state found in all four out-group genera, unless otherwise stated. Note that *Pseudophotopsis* also has a large proportion of apomorphic character states and quite often has the derived state of a character when the other three out-group genera have the plesiomorphic state.

RESULTS

Table 1 shows the distribution of character states among the genera of Ticoplinae. The single most-parsimonious tree found (Fig. 26) has *Areotilla* and *Nanomutilla* as sister groups; the same tree was found using implied weighting. This tree has length = 26 steps, consistency index (CI) = 0.88 and retention index (RI) =

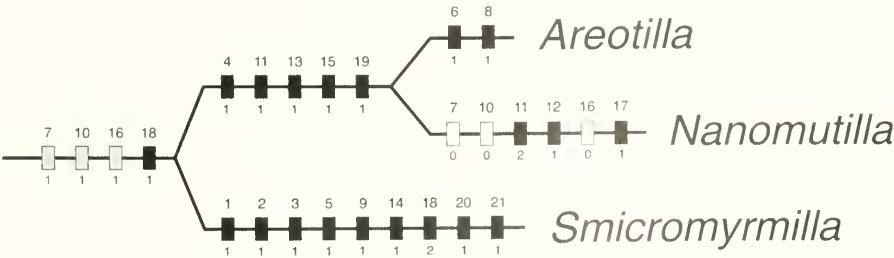


Fig. 26. Single most-parsimonious cladogram of genera of Ticoplinae (length 26, consistency index 0.88, retention index 0.62). Character numbers above, states below hash marks. Hash-mark shading: black = unique derivation, grey = convergent derivation, white = reversal.

0.62. Under fast (accelerated transformation) optimisation, the 23 derived states comprise 14 autapomorphies, 5 unique synapomorphies for *Areotilla* and *Nanomutilla*, 1 unique synapomorphy for all three genera, and 3 homoplasies (characters 7M, 10M and 16M). An alternative tree with *Areotilla* and *Smicromyrmilla* as sister groups (supported by 3 synapomorphies) is two steps longer and has a much lower RI (length = 28, CI = 0.82, RI = 0.37); the other alternative tree with *Nanomutilla* and *Smicromyrmilla* as sister groups is not supported by any synapomorphies and is even longer (length = 31, CI = 0.74, RI = 0.00).

From the results, it is evident that *Areotilla* and *Nanomutilla* are the most closely related cladistically, and are distinct from *Smicromyrmilla* in several respects. The degree of difference seen between the two groups is similar to, if not greater than, that between the tribes of Sphaerophthalminae or Mutillinae (Brothers 1975) or those of Myrmosinae (Brothers 1999). This contrasts with the opinion of Brothers (1975) who had seen far fewer representatives of these genera and who felt that there were no marked groupings between them. We thus consider that recognition of two tribes, as proposed by Argaman (1988), is warranted despite the fact that both contain relatively few species when compared with most other tribes of Mutillidae.

CHARACTERISTICS OF SUBFAMILY AND TRIBES

Previous descriptions or diagnoses of the subfamily and tribes, such as those by Brothers (1975, 1993), Suárez (1975) and Argaman (1988), are incomplete or inaccurate, mainly because those authors had access to far fewer species than we were able to examine. The following descriptions are followed by comments indicating differences from previous attempts.

Ticoplinae Nagy 1970 (= *Nanomutillinae* Suárez 1975).—No felt line on second

metasomal tergum. Macropterous males with fully articulating meso-metapleural suture (i.e., no ventral bridge-like fusion between meso- and metapleuron), posteriorly convex mesopleural margin, petiolate second submarginal cell in the forewing, and volsella lacking digitus (i.e., only cuspis present). Females and microppterous/apterous males with mesosoma widest posteriorly (seldom with sides more or less parallel) with one or more weak to strong teeth or spines at posterolateral angle, posterolateral margin of pronotum indistinguishably fused with mesopleuron (except in males with pronotum articulating with mesothorax), and distance from humeral angle to pronotal spiracle at least as long as that between pronotal and propodeal spiracles (except in males with articulating pronotum where it may be shorter).

Ticoplini Nagy 1970 (= *Nanomutillini* Suárez 1975).—Eye strongly pubescent; antennal tubercles closely approximated basally but separate, not joined by a straight transverse ridge, scarcely protruding; pronotum smoothly and evenly convex over anterior declivity, without a transverse carina; propodeum with disc and declivity distinct; second metasomal sternum without felt line. Males with notauli usually distinct (often faint and sometimes absent in *Nanomutilla*); scutellum not apically produced; propodeum with three or five large fields covering entire surface of disc and defined by well developed carinae; metasomal sternum 2 with a short median longitudinal carina basally; penis valve $> 0.75\times$ as long as paramere. Females with at most one short spine on posterolateral angle of propodeum at apex of lateral oblique transverse carina; 'auricle' at base of first metasomal tergum merely a small rounded protuberance; no defined pygidial area.

Smicromyrmillini Argaman 1988.—Eye pubescence absent although pores and/or very sparse minute setae may be present; antennal tubercles fused basally, joined by

a small straight transverse ridge, distinctly protruding; pronotal dorsum sharply separated from anterior declivity, with junction angular and marked by a transverse carina; propodeum with disc and declivity evenly merging, not distinct; second metasomal sternum with well developed lateral felt line. Macropterous males lacking notauli; scutellum apically produced over metanotum; propodeum with three poorly defined anterior fields and many reticulations forming mini fields over posterior half; metasomal sternum 2 lacking median longitudinal carina; penis valve $< 0.60\times$ as long as paramere. Females and microp- terous/apterous males with at least two spines on posterolateral angle of propo- deum, lacking lateral oblique carina to base of spine; ‘auricle’ at base of first me- tasomal tergum forming a strong lamel- late or spinose protuberance; glabrous py- gidial area well defined.

Suárez (1975) included only *Nanomutilla* (females) in his subfamily Nanomutillinae. Various of the features that he high- lighted as being characteristic of the group (as compared with *Smicromyrmilla* which he placed in the Myrmillinae) are thus re- stricted to that genus, and in particular to a species which he considered to be *N. vaucheri*. Non-differentiated pubescence on the body was thought characteristic, as compared with the varied pubescence generally forming patterns in other Mutillidae; although this is particularly true of *Nanomutilla*, it is approached in *Areotilla* but is not particularly significant since it occurs elsewhere in the Mutillidae also. The peculiar ‘bethyloid’ or ‘proctotrupoid’ body form was also highlighted, but this is not true of *Areotilla*.

Argaman (1988) also included only *Na- nomutilla* (and ‘*Ticopla*’), but both sexes, in the Ticoplini. He thought that the flagel- lomeres were different in shape and struc- ture from those in *Smicromyrmillini*, that the pronotum (in the female) differed in the number of lateral pits and that the de- gree of production of the apex of the pro- podeum at the articulation with the me- tasoma differed. We have found that fla- gellomere shape varies across both tribes and also according to viewpoint, that the development of pits on the pronotum varies considerably and that the produc- tion of the propodeal lobe also varies and is not significantly different from the con- dition in most other Mutillidae. Argaman remarked on the fact that the second me- tasomal tergum is longer than wide in fe- male Ticoplini, but this is true only of some *Nanomutilla* and not of *Areotilla*. For male Ticoplini, Argaman noted the pres- ence of a single complete ridge on the scape, but this is true of *Nanomutilla* only (see our character 7, below).

Neither Suárez (1975) nor Argaman (1988) mentioned the pubescence of the eye in female Ticoplini, presumably be- cause it is difficult to see in *Nanomutilla* specimens, which are very small. Both au- thors noted the absence of ‘auricles’ (Brothers 1975) at the base of the metasoma, but they are actually present although inconspicuous.

For the *Smicromyrmillini*, Argaman (1988) made much of the carinate anterior margin of the mesoscutum in the male, considering this a unique character in Hy- menoptera; such a carina is certainly pre- sent in some species of *Smicromyrmilla* but many other species have no trace of it.

KEY TO TRIBES AND GENERA OF TICOPLINAE

[Note: We consider *Eosmicromyrmilla* and *Hindustanilla* doubtfully distinct from *Smicromyrmilla*; *Cameronilla* is probably misplaced in Ticoplinae, see above, and is therefore omitted from this key.]

- 1 (a) Wings well developed (male) 2
- (b) Wings absent or rudimentary (female, rarely male) 4

- 2 (a) Eye pubescence distinct; scutellum apex not overhanging metanotum; propodeal disc covered by 3 or 5 large fields each surrounded by well developed carinae; metasomal sternum 2 without felt line (Ticoplini) 3
- (b) Eye pubescence absent; scutellum apex produced and overhanging metanotum; propodeum with 3 very weakly defined anterior fields and many reticulations forming mini fields over posterior half; metasomal sternum 2 with well developed lateral felt line (Smicromyrmillini) .. *Smicromyrmilla* (including *Eosmicromyrmilla* and *Hindustanilla*)
- 3 (a) Tegula elongate and reniform, $> 0.75\times$ as long as mesoscutum; propodeal disc with 5 fields; paramere apex very strongly curved ventrally *Areotilla*
- (b) Tegula oval, $< 0.60\times$ as long as mesoscutum; propodeal disc with 3 fields; paramere almost straight *Nanomutilla*
- 4 (a) Eye pubescence distinct; metasomal sternum 2 without felt line; propodeum with disc and declivity distinct, separated laterally by an oblique transverse carina ending in a single small posterolateral tooth; no distinct pygidial area (Ticoplini) 5
- (b) Eye pubescence absent; metasomal sternum 2 with lateral felt line; propodeum with disc and declivity smoothly merging, without any lateral transverse carinae and with 2 or more posterolateral teeth or spines; female with distinct glabrous pygidial area (Smicromyrmillini) *Smicromyrmilla* (including *Eosmicromyrmilla* and *Hindustanilla*)
- 5 (a) Body length > 4 mm; eye large relative to head (ratio of eye height to head height > 0.6); eye with > 400 small ommatidia; second metasomal tergum about $1.5\times$ as wide as long *Areotilla*
- (b) Body length < 3 mm; eye small relative to head (ratio of eye height to head height < 0.5); eye with < 100 large ommatidia; second metasomal tergum about as wide as long *Nanomutilla*

GEOGRAPHICAL DISTRIBUTION

The subfamily occurs in the southern Palaearctic, Afrotropical and Oriental Regions. The tribes differ in distribution only in that Ticoplini have not yet been found in the Oriental Region. Brothers (1975) proposed that the Ticoplinae arose in eastern Central Africa, and from there spread northwards to the Mediterranean region, southwards into southern Africa and eastwards to the Indian plate, while it was still in contact with Africa or very close to it, i.e. at least about 80 million years ago (Smith, Hurley and Briden 1981). However, this does not account for the apparent absence of Ticoplinae from Madagascar, as reflected by at least two recent collecting expeditions there (from the Natural History Museum (London) and the University of Kansas) which have failed to come up with any specimens, despite their emphasis on Hymenoptera.

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APPENDIX 1

Characters used for cladistic analysis of genera of Tico-plinae. Suffixes: B = applicable to both sexes, F = female only, M = male only. Primitive states coded as 0, derived states as 1 or 2. All characters considered additive.

1B. Eye pubescence. 0 = Present, visible at 20× magnification. 1 = Absent, although pores and/or very sparse short setae may be distinguishable under high magnification. (State 0 is found in most Tiphidae (Brothers 1975), Fedtschenkiinae (Sapygidae), *Myrmosa* and

- Myrmosula*; since almost all *Pseudophotopsis*-*dinae* and all other mutillids lack eye pubescence, state 1 has most likely evolved independently within the *Ticoplinae*.)
- 2B. Antennal tubercles. 0 = Separate although closely approximated, not joined by a straight transverse ridge, scarcely protruding. 1 = Fused medially, joined by a straight transverse ridge, distinctly protruding.
- 3B. Pronotum, dorsal and anterior faces. 0 = Smoothly and evenly merging, without a transverse carina. 1 = Sharply separated by a distinct transverse carina, at least laterally. (Of the out-group genera, *Pseudophotopsis* has state 0, *Dasylabris* has state 1, while *Myrmosa* and *Myrmosula* appear variable. As none of the out-group taxa have state 1 developed as strongly as in the in group, this state is considered apomorphic.)
- 4B. Propodeum, disc and declivity distinction. 0 = Smoothly merging, not distinct. 1 = Distinct, in different planes.
- 5B. Felt line on metasomal sternum 2. 0 = Absent. 1 = Present. (Brothers (1975) stated that "... the tendency toward development of [tergal] felt lines is considered to have been established after the divergence of the *Myrmosinae*" which have neither tergal nor sternal felt lines (like the *Rhopalomutillinae*, in which traces of tergal felt lines are present in only a few males). Referring to the phylogeny of the *Mutillidae* (Fig. 1) this indicates that the actual development of tergal felt lines has apparently occurred on two occasions, once in *Pseudophotopsis* and again on internode 4–5. Similarly, when considering sternal felt lines, which are present in *Pseudophotopsis*, *Smicromyrmilla* and sporadically within taxa derived above *Rhopalomutillinae*, it is most parsimonious to consider felt lines to have been developed independently on several occasions. Thus, absence of felt lines is plesiomorphic for the *Ticoplinae*.)
- 6M. Eye, inner margin shape. 0 = Shallowly emarginate at or below mid height. 1 = Strongly notched above mid height.
- 7M. Scape, ventral longitudinal carinae. 0 = One (lateral). 1 = Two (mesal and lateral). (Primitively, there is only one longitudinal carina on the scape, or none. Although *Dasylabris* has two carinae, this appears to have been derived separately in many higher taxa.)
- 8M. Ratio of tegula length to mesoscutum length. 0 = < 0.60 . 1 = > 0.75 .
- 9M. Scutellum, posterior margin. 0 = Abutting metanotum. 1 = More or less lamellate and overhanging metanotum.
- 10M. Scutellum and dorsellum, profile. 0 = On essentially the same plane. 1 = On two distinct planes. (State 0 is found in all out-group taxa except for *Dasylabris*.)
- 11M. Propodeum, fields. 0 = Three small fields on anterior half defined by weakly developed carinae, many mini fields on posterior half. 1 = Five large fields defined by very well developed carinae. 2 = Three very large fields defined by well developed carinae. (This character was treated as additive because the states are complex, with state 1 appearing to be intermediate between 0 and 2.)
- 12M. Propodeum, extent of disc and declivity. 0 = Disc about as long as declivity height. 1 = Disc at least $1.5\times$ as long as declivity height.
- 13M. Metasomal sternum 2, short median longitudinal basal carina. 0 = Absent. 1 = Present.
- 14M. Hypopygium, apical margin. 0 = Shallowly emarginate or notched. 1 = With deep narrow median split. (State 0 is the more similar to the conditions in all the out-group taxa; state 1 is unique in *Mutillidae*.)
- 15M. Penis valve, relative length. 0 = $< 0.60\times$ as long as paramere. 1 = $> 0.75\times$ as long as paramere. (State 0 is found in *Myrmosa* and *Pseudophotopsis*, despite the highly derived, spinose state of the penis valve in the latter subfamily; while *Dasylabris* has state 1, this has probably been separately derived.)
- 16M. Paramere curvature. 0 = Straight. 1 = Apex strongly curved ventrally.
- 17F. Eye size. 0 = Large (eye height $> 0.60\times$ head height) with > 400 small ommatidia. 1 = Small (eye height $< 0.50\times$ head height) with < 100 large ommatidia.
- 18F. Propodeum, posterolateral spines. 0 = None. 1 = One. 2 = At least two. (None of the out-group genera has spines on the declivity; the development is postulated as progressive, the character thus being regarded as additive.)
- 19F. Propodeum, lateral carinae. 0 = No distinct carinae. 1 = Distinct obliquely transverse carinae extending posterolaterally.
- 20F. 'Auricle' (Brothers 1975) at base of first me-

tasomal tergum. 0 = Forming slight rounded protuberance. 1 = Forming prominent lamellate or spinose protuberance. (These structures are absent in females of Myrmosinae, fairly well developed in Pseudophotopsidinae and well developed elsewhere although generally not so prominently as in *Smicromyrmylla* females.)

21F. Pygidium. 0 = No defined pygidial area or plate. 1 = Distinct glabrous pygidial area present. (There is no pygidial area in Myrmosinae, but such an area is present in most other Mutillidae, including the other out-group representatives, although it varies considerably in form. The suggested polarity was thus considered the more likely to be correct.)